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Event-related potentials reveal the development of stable face representations from natural variability

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Event-related potentials reveal the development of stable face representations from natural variability

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Running head: Developing stable face representations

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Keywords: Face recognition, face learning, stable representations, event-related potentials,

N250

Abstract

Natural variability between instances of unfamiliar faces can make it difficult to reconcile two images as the same person. Yet for familiar faces, effortless recognition occurs even with considerable variability between images. To explore how stable face representations develop, we employed incidental learning in the form of a face sorting task. In each trial, multiple images of two facial identities were sorted into two corresponding piles. Following the sort, participants showed evidence of having learnt the faces, performing more accurately on a matching task with seen than unseen identities. Furthermore, ventral temporal event-related potentials were more negative in the N250 time range for previously-seen than previously-unseen identities. These effects appear to demonstrate some degree of abstraction, rather than simple picture learning, as the neurophysiological and behavioural effects were observed with novel images of the previously-seen identities. The results provide evidence of the development of facial representations, allowing a window onto natural mechanisms of face learning.

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Whereas behavioural studies provide information about the outcome of a cascade of cognitive sub-processes, event-related brain potentials (ERP) allow the examination of these neuro-cognitive sub-stages in more detail (see e.g., Luck, 2005). ERPs are voltage changes in the human electroencephalogram (EEG), thus reflecting the summed activity of post-synaptic potentials (see e.g., Jackson & Bolger, 2014), which are time-locked to certain events such as the presentation of a visual stimulus. ERP waveforms consist of a series of positive and negative components or peaks, which represent neural correlates of specific perceptual and cognitive processing stages. For instance, all visual stimuli elicit a positive-going P1 component, which peaks at occipital channels about 100 ms after stimulus onset. The P1 reflects early visual processes, as it is highly sensitive to low-level stimulus characteristics, such as luminance or contrast (e.g., Luck, 2005).

The earliest ERP component closely related to face rather other visual object processing is the N170 (Bentin et al., 1996; Eimer, 2011), a negative deflection peaking at occipito-temporal channels roughly 170 ms after stimulus onset. N170 is often interpreted to reflect the structural encoding of faces or the detection of a face-like pattern (Eimer, 2000; Schweinberger & Burton, 2003; Amihai, Deouell, & Bentin, 2011), i.e., processing stages prior to the identification of an individual face. In line with this, a number of studies found no difference in N170 amplitude for familiar relative to unfamiliar faces (Bentin & Deouell, 2000; Eimer, 2000; Schweinberger et al., 2002; Henson et al., 2003). Other studies, however, found larger N170 amplitudes for familiar relative to unfamiliar faces (experiment 2 in Wild-Wall, Dimigen & Sommer, 2008; Caharel et al., 2005, 2006), or larger amplitudes for unfamiliar relative to familiar faces (Marzi & Viggiano, 2007). Accordingly, the question whether N170 is sensitive to face familiarity is not entirely resolved. It should be noted, however, that even those studies supporting this suggestion are not consistent regarding the direction of a potential N170 familiarity effect, and that such effects are typically small.

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1 An ERP component showing clear sensitivity to facial familiarity is typically
2 observed to peak approximately 250 ms following stimulus onset. Immediate repetitions of
3 familiar faces have been shown to result in increased negativity relative to non-repetitions at
4 occipito-temporal scalp sites (Begleiter, Porjesz & Wang, 1995; Schweinberger, Pfütze &
5 Sommer, 1995), an effect known as N250r (r for repetition). While an N250r is also observed
6 for unfamiliar faces, the effect is much smaller (Schweinberger et al., 1995), and largely
7 restricted to the repetition of identical images (see Zimmermann & Eimer, 2013).
8 Interestingly, an N250r for familiar faces has been shown even when different images of the
9 same identity are presented as the second stimulus (Schweinberger, Pickering, Jentzsch,
10 Burton & Kaufmann, 2002). Increases in negativity here are smaller than when the same
11 image is repeated, suggesting that the effect is in part image-sensitive. Similarly, a degree of
12 viewpoint-independence of the N250r may develop after face learning (Zimmermann &
13 Eimer, 2013). While it has been a considerable challenge to experimentally separate the
14 image-independent and image-specific parts of the N250r (for promising approaches, see
15 Bindemann et al., 2008, and Doerr et al., 2011), one might argue that the image-independent
16 part of the N250r reflects the transient activation of stable representations – akin to face
17 recognition units (see Bruce & Young, 1986).

18 More recently, a similar negativity has been observed with intervening faces between
19 identity repetitions, which shares a similar onset to N250r, but extends until around 400ms
20 post stimulus onset (e.g. Itier & Taylor, 2004). Thus, repetition effects have been analysed
21 separately in two subsequent time windows (e.g., Kaufmann et al., 2009), representing an
22 ‘early’ (app. 200 – 280 ms) and a ‘late N250’ (app. 280 – 400 ms), respectively (Wiese,
23 2012). Importantly, the N250 effect is evident for *familiar* faces when images of different
24 identities appear between repetitions, while in the case of *unfamiliar* faces, the presence of
25 different identities between repetitions eliminates the effect (Pfütze, Sommer, &

Schweinberger, 2002). Indeed, Itier & Taylor (2004) demonstrated that seeing the same face multiple times (with non-immediate repetitions) produces a more long-term N250. Studies on face repetition therefore suggest that the more negative N250 for repeated faces reflects the transient activation of an individual face representation, with stronger activations for better-known faces. Generally in line with this idea, a larger N250 has also been observed for famous relative to unfamiliar faces (Gosling & Eimer, 2011).

Of most relevance to the present experiment, N250 is sensitive to face learning. More specifically, following learning, pre-experimentally unfamiliar faces show an enhanced N250 that is equivalent to highly familiar faces (Pierce, Scott, Boddington, Droucker, Curran & Tanaka, 2011; Tanaka, Curran, Porterfield & Collins, 2006). Importantly, Kaufmann and colleagues observed an increased N250 for different instances of the learned identities, showing that the effect was not due to the formation of a pictorial representation (Kaufmann et al., 2009). Moreover, in this study N250 amplitude further increased with increasing familiarity of the faces over different experimental blocks. Therefore, a larger N250 to different-image, non-immediate repetitions of faces reflects an index of familiarity that can be used to track the establishment of face representations (Kaufmann et al., 2009). At the same time, increasing N250 amplitudes in the course of learning appear to reflect the acquisition of a stable face representation, independent of the repetition of specific images.

Whether and to what extent N250r as measured in repetition priming paradigms and the N250 face learning effect reflect the same underlying processes is not entirely clear at present and of substantial theoretical interest (see also Schweinberger & Neumann, in press). As described above, N250r is typically measured as the difference between repeated and non-repeated familiar faces, and therefore likely reflects facilitated access of a well-established representation due to its pre-activation by the prime. At the same time, the N250 effect in learning experiments is usually measured as the difference between newly learnt and

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1 unfamiliar faces. It probably reflects access to a newly formed representation for the learnt
2 faces, whereas no corresponding representation exists for unfamiliar faces. Accordingly, this
3 effect may be similar, although probably less pronounced (see below), to the difference in
4 N250 between famous and unfamiliar faces (Gosling & Eimer, 2011), which may also reflect
5 accessing a representation of an individual face in the former but not in the latter case.

6 As noted earlier, face learning involves the development of representations that allow
7 the recognition of faces under highly variable conditions. Such variability might be
8 encountered across a complex combination of dimensions. For example, a face may appear
9 different between encounters because of textural differences due to lighting, health, and
10 tiredness changes, in addition to differences because of changes in viewpoint, expression, and
11 distance from the observer. Whereas some ERP studies on face learning did not take any of
12 these dimensions into account (Tanaka et al., 2006; Pierce et al., 2011), as identification of
13 the newly learnt face was tested with the same image at all occasions, Kaufmann and
14 colleagues (2009) observed an enhanced N250 for newly learnt faces for previously unseen
15 instances. Another recent study by Schulz, Kaufmann, Kurt, and Schweinberger (2012)
16 extended these findings by showing distinct contributions of distinctiveness for face learning
17 and its correlate in the N250. However, in both studies, variability between images was rather
18 restricted to head turning, small differences in viewpoint, or speaking, but otherwise
19 experimentally constrained to maintain other dimensions of variability. At the same time, it
20 has been shown that high-quality, full-frontal images of unfamiliar people, taken on the same
21 day but with different cameras and under different lighting conditions, are relatively hard to
22 match (Bruce et al., 1999). Sources of image variability in this latter study were quite
23 different from those in previous ERP studies on face learning, which therefore only
24 superficially, and incompletely, capture the apparent changes of an unfamiliar person's
25 appearance in real life.

1 Interestingly, previous studies using adaptation techniques in functional brain imaging
2 found a sensitivity of the so-called fusiform face area (FFA) for facial identity when different
3 images with limited variability (i.e., changes in viewpoint) were used (Ewbank & Andrews,
4 2008). At the same time, FFA was not sensitive to identity when images with natural
5 variability were presented (Davies-Thompson et al., 2009), although a more anterior
6 subregion of fusiform gyrus has been reported to exhibit identity-sensitive responses for such
7 face images (Eger, Schweinberger, Dolan, & Henson, 2005). It is therefore important to
8 understand whether the N250 learning effects observed in studies with limited variability
9 extend to variability that might naturally be experienced, i.e. across ‘ambient images’
10 (Jenkins et al, 2011; Sutherland et al, 2013; see Figure 1). Jenkins et al. (2011) recently
11 demonstrated that sorting naturally varying images is remarkably difficult for unfamiliar
12 faces. In their task, unfamiliar observers were asked to sort 40 ambient images into as many
13 identities as they perceived. The most common number of identities perceived was nine, even
14 though only two identities were actually present. Accordingly, telling unfamiliar faces apart
15 seems to be much easier than telling unfamiliar faces together. Familiar observers, on the
16 other hand, sorted the identities quickly and accurately, with seemingly no difficulty,
17 reflecting the ability to accommodate entirely novel instances once a stable representation has
18 been established.

19 The present experiment examines how the formation of stable representations affects
20 the neural processing of newly learnt faces. To do this, we used ‘ambient images’ and an
21 incidental learning technique, based on the sorting procedure of Jenkins et al. (2011). This
22 reflects a further critical difference to previous ERP studies on face learning, which used
23 explicit learning tasks. The use of an implicit learning task is arguably closer to face learning
24 in daily life, as we usually do not explicitly try to encode the faces of the people we have just
25 met. Observers were asked to sort 40 unfamiliar face images of two different people into

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1 separate piles for each identity. However, unlike the Jenkins et al study, we instructed our
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3 participants that only two different people were present. Under these constraints, naturally
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5 varying instances are sorted into their respective identities with very few misidentification
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8 errors (Andrews et al., 2015). Therefore, the constraint of being told the correct number of
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10 identities appears to enable the incidental learning of these identities during sorting.
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14 To determine whether resulting representations for these identities can be observed in
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16 ERP familiarity correlates, we investigated any putative differences between novel, newly
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18 learnt and pre-experimentally familiar (famous) faces in the N250. We assumed that face
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20 learning, as implemented in the present study, would result in the establishment of a stable
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22 representation that would on the one hand not be available for novel faces, but that would on
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24 the other hand not be as refined as the representation of highly familiar faces. Accordingly,
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26 N250 for newly learnt faces was expected to lie in-between the N250 for famous and novel
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28 faces. Importantly, we also investigated whether any observable differences in neural
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30 processing exist between images of learnt identities that were seen during learning, and
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32 completely new instances of learnt faces that have not been seen before. If the sorting task
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34 results in the establishment of stable representations, we hypothesised that N250 would be
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36 more negative for learnt than novel faces. Moreover, any potential difference in the same-
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38 image versus different-image conditions would inform about the extent to which the observed
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40 N250 learning effect reflects image-dependent or image-independent learning. At the same
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42 time, no difference between the images that were seen in the earlier learning phase and
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44 previously unseen images of the learnt identities would be strongly indicative of the implicit
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46 formation of stable (rather than image-dependent) representations of facial identities (Burton
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48 et al., 2005; Burton, Jenkins, & Schweinberger, 2011). Whereas some studies found learning
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50 effects in the early N250 (Kaufmann et al., 2009), others observed effects that extended well
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1 into the later N250 time range (Schulz et al., 2012). It was therefore not clear whether
2 learning effects in the present study would occur in the early or late N250.

3 In addition, to estimate behavioural effects of face learning, and to ascertain their
4 relationship to any ERP findings, we measured performance in a subsequent perceptual
5 matching task. This task indicates differences in levels of familiarity, such that highly
6 familiar faces are matched with greater accuracy than less familiar faces (Clutterbuck &
7 Johnston, 2002; 2005).

8 9 **Methods**

10 **Participants**

11 Twenty-four (19 female) undergraduate students with a mean age of 21.95 years (SD
12 = 3.42, range = 18-30) from the Friedrich Schiller University of Jena participated in the
13 experiment for course credit or a reimbursement of 5 €/h. All participants reported normal or
14 corrected to normal vision, and reported no previous neurological or psychiatric conditions.
15 All were native German speakers and all were right-handed (as measured by the Edinburgh
16 Handedness Inventory; Oldfield, 1971). All participants gave written informed consent to
17 participate.

18 **Design & materials**

19 There were three components to the current design. All participants completed an
20 initial sorting task, followed by an ERP task, finishing with a face matching task. All portions
21 of the design were manipulated within-subjects.

22 Stimuli were 85 images each of 6 identities unfamiliar to our participants (Dutch
23 celebrities; Chantal Janzen, Gigi Ravelli, Hanna Verboom, Nicolette Kluijver, Renate
24 Verbaan and Wendy van Dijk), 20 images each of 2 pre-experimentally familiar celebrities
25 (Cameron Diaz, Heidi Klum), and 12 images of different butterflies (used as target stimuli

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during the ERP task, see below). Images were obtained from a Google Image search, and were the first unique images where the face/butterfly occupied at least 190 x 285 pixels, and where faces were roughly front-facing. These were then size-adjusted and cropped to 190 x 285 pixels in height, and converted to greyscale.

For each unfamiliar identity, three image sets were randomly selected, comprising two sets of 20 images each to be used in the sorting and EEG tasks and a further set of 45 images to be used in the matching task (match Set). Each identity was paired with another, so that two identities always co-occurred (unfamiliar set 1 consisted of Chantal Janzen with Hanna Verboom, unfamiliar set 2 consisted of Gigi Ravelli with Renate Verbaan, and unfamiliar set 3 consisted of Nicolette Kluijver with Wendy van Dijk). There were therefore 3 pairs of identities; for each pair of faces, there were 40 images in set A, 40 images in set B, and 90 images in set C. Mean luminance for all face stimuli to be used in the EEG portion of the study was calculated using image analysis software (ImageJ; Schneider, Rasband & Eliceiri, 2012) and entered into a one-way between subjects ANOVA (factor levels famous set, unfamiliar set 1-A, unfamiliar set 1-B, unfamiliar set 2-A, unfamiliar set 2-B, unfamiliar set 3-A, unfamiliar set 3-B). Results from this analysis revealed no differences in mean luminance between the sets ($F(6, 273) = 1.00, p > .05, \eta p^2 = .02$).

For the sorting task, the 80 images (40 in set A, 40 in set B) of each of the 3 unfamiliar ID pairs were printed at a size of 3 x 4 cm, at maximum DPI and laminated. The ID pair used for the sorting task was counterbalanced across participants, so that each of the 6 unfamiliar face sets (3 ID pairs x 2 image sets [A, B]) were seen by an equal number of participants during the sorting task.

For the ERP task, 172 trials were completed in total. These were 40 trials for same images of the IDs seen in the sorting task (seen-in-sort-sIMG), 40 trials for different images of the IDs seen in the sorting task (seen-in-sort-dIMG), 40 famous ID trials (famous), 40

1 previously unseen unfamiliar ID trials (new-to-ERP), and 12 butterfly trials, which were not
2 analysed. Images were presented sequentially for 1000ms at 190 x 285 pixels in the centre of
3 the screen. Trials were preceded by a fixation with a randomly selected duration (ranging
4 from 700-1300ms in 100ms intervals; $M = 1000\text{ms}$). Participants sat at a distance of 90cm
5 from the screen, with head position maintained with an adjustable chinrest. This resulted in a
6 visual angle of approximately $4.04^\circ \times 6.38^\circ$ for each image. Image order was randomly
7 selected for each participant.

8 For the matching task, 180 trials were completed in total. These were 15 same-ID and
9 15 different-ID trials for each of the 2 IDs that were first seen in the sorting task (seen-in-
10 sort), 15 same- and 15 different-ID trials for each of the 2 IDs that were first seen in the ERP
11 task (seen-in-ERP), and 15 same- and 15-different ID trials each for 2 previously unseen
12 unfamiliar IDs (new-to-match). Each image was presented at 190 x 285 pixels, with image
13 pairs presented side-by-side.

14 **Procedure**

15 Participants were prepared for the EEG portion of the experiment prior to the sorting
16 task. They were then handed a pile of shuffled cards of two identities, and asked to sort the
17 images into separate piles so that all the images of the same person were together. They were
18 told that only two identities were present, and that they should generate only two piles. They
19 were also encouraged to place images of the same person next to one another, so they could
20 see all images at the same time. There was no time restriction, and participants were able to
21 move images freely back and forth between piles before settling on their final decision.

22 In the ERP task, participants were presented with sequentially presented images,
23 which remained on screen for 1s and were preceded by a fixation. Participants were required
24 to respond using a keypress when a butterfly was presented, but to withhold any response
25 following the presentation of faces. Speed and accuracy of responses was stressed.

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1 In the face matching task, participants were presented with pairs of faces, and were
2 required to indicate via keypresses whether pairs were of the same person, or two different
3 people. There was no time restriction, and participants were encouraged to respond as
4 accurately as possible.

5 **EEG recording and analyses**

6 EEG was recorded from 32 active sintered Ag/Ag–Cl electrodes using a Biosemi
7 Active II system (BioSemi, Amsterdam, Netherlands). Please note that BioSemi systems
8 work with a “zero-Ref” set-up with ground and reference electrodes replaced by a CMS/DRL
9 circuit (cf. <http://www.biosemi.com/faq/cms&drl.htm> for further information). EEG was
10 recorded continuously with a 512-Hz sample rate from DC to 155 Hz. Recording sites
11 corresponded to an extended version of the 10–20-system (Fz, Cz, Pz, Iz, FP1, FP2, F3, F4,
12 C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10,
13 PO9, PO10, I1 and I2). Blinks were corrected using the algorithm implemented in BESA
14 5.1.8 (see Berg & Scherg, 1994). EEG was then segmented from –200 ms until 1000ms
15 relative to stimulus onset, with the first 200 ms serving as a baseline. Artifact rejection was
16 carried out using an amplitude threshold of 100µV and a gradient criterion of 50µV.
17 Remaining trials were recalculated to average reference, averaged according to experimental
18 condition and digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift). In the
19 resulting waveforms, mean amplitude of the P1 (85-115 ms) was analyzed at O1/O2, while
20 mean amplitudes of N170 (130-160 ms), and early and late N250 (240-280 ms, 280-400ms)
21 were analyzed at electrode sites P9/P10, PO9/PO10, and TP9/TP10 as in previous studies on
22 face learning (Kaufmann et al., 2009). The mean number of trials was 35.8 in the seen-in-
23 sort-sIMG (SD = 4.9; range = 24 - 40), 35.6 in the seen-in-sort-dIMG (SD = 4.8; range = 22 -
24 40), 36.3 in the famous (SD = 4.4; range = 24 – 40), and 35.5 in the new-to-ERP conditions
25 (SD = 5.0; range = 23 - 40), respectively.

Results

Sorting task

Intrusion errors were calculated for each participant. We define intrusion errors as an instance of one ID appearing in a pile containing mostly images of the other ID. The median number of errors from sorting the 40 images was 0.5 (mode = 1; range = 0 - 19), and 6 participants sorted the identities perfectly.

Matching task

Correct responses were entered into a one-way repeated measures ANOVA with 3 levels (exposure; new-to-match, seen-in-ERP, seen-in-sort). Data from two participants were missing due to technical errors, leaving data from 22 participants. The resulting output revealed a significant main effect of exposure ($F(2, 42) = 10.41, p < .001, \eta^2 = .33$). Tukey's HSD showed this effect was due to a significant difference between new-to-match IDs and seen-in-sort IDs ($M = .80 \pm 0.03 \text{ SEM}$ and $M = .89 \pm 0.03 \text{ SEM}$, respectively; $p < .05$), and also between new-to-match IDs and seen-in-ERP IDs ($M = .80 \pm 0.03 \text{ SEM}$ and $M = .85 \pm 0.03 \text{ SEM}$, respectively; $p < .05$).

ERP task

During the EEG task, participants detected all target stimuli. Two participants wrongly pressed the response key when a face was presented, but both only in one trial. Mean response time for correct responses was 509.5 ms ($\pm 50.8 \text{ SD}$).

ERP waveforms are depicted in Figure 2, and scalp-topographical voltage maps of exposure effects relative to the novel condition are shown in Figure 3. In the interests of stringency and readability, only effects that involve the factor 'exposure' will be reported in-text. A complete list of all effects from P1 and N170 can be found in Table 1, while a complete list of all effects from Early and Late N250 can be found in Table 2.

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P1

P1 amplitude was analysed using a 4 (exposure; new-to-ERP, seen-in-sort-sIMG, seen-in-sort-dIMG, famous) x 2 (hemisphere; left, right) repeated measures ANOVA, which revealed no significant effect of exposure ($F(3, 69) = 1.11, p = .350, \eta^2 = .046$), or interaction between exposure and hemisphere ($F(3, 69) = 2.42, p = .073, \eta^2 = .10$). This finding indicates that potential low-level differences between faces in the different experimental conditions did not affect the ERP results.

N170

N170 amplitude was analysed using a 4 (exposure; new-to-ERP, seen-in-sort-sIMG, seen-in-sort-dIMG, famous) x 2 (hemisphere; left, right) x 3 (site; TP, P, PO) repeated measures ANOVA. Again, there was no significant effect of exposure ($F(3, 69) = 1.01, p = .393, \eta^2 = .042$), and no interaction between hemisphere and exposure ($F(6, 138) = 1.94, p = .079, \eta^2 = .078$; see Figure 2).

Early N250

A corresponding ANOVA for the early N250 time window revealed a significant main effect of exposure ($F(3, 69) = 4.46, p = .010, \eta^2 = .163$). There were no significant interactions either between exposure and site ($F(6, 138) = 1.12, p = .354, \eta^2 = .046$), or between exposure and hemisphere ($F(6, 138) = 1.92, p = .135, \eta^2 = .077$), although somewhat larger exposure effects were seen over the right hemisphere. There was also no significant three-way interaction between hemisphere, site and exposure ($F(6, 138) = 1.09, p = .373, \eta^2 = .045$). Follow-up contrasts on the main effect showed this effect to be driven by a difference between new-to-ERP and famous IDs ($F(1, 23) = 18.36, p < .001, \eta^2 = .444$), with famous IDs being significantly more negative. There was also a trend for seen-in-sort-dIMG to show more negative amplitudes than new-to-ERP IDs ($F(1, 23) = 3.09, p = .092, \eta^2 = .119$), whereas the difference between seen-in-sort-sIMG and new-to ERP IDs was not

significant ($F(1, 23) = 2.09, p = .162, \eta^2 = .083$). At the same time, famous IDs elicited more negative amplitudes than both seen-in-sort-sIMG ($F(1, 23) = 5.13, p = .033, \eta^2 = .182$) and seen-in-sort-dIMG conditions ($F(1, 23) = 4.92, p = .037, \eta^2 = .176$).

Late N250

A corresponding analysis was conducted in the 280 – 400ms time window. This revealed a significant main effect of exposure ($F(3, 69) = 15.30, p < .001, \eta^2 = .400$). There were no significant interactions either between exposure and site ($F(6, 138) = 0.76, p = .603, \eta^2 = .032$), or between exposure and hemisphere ($F(6, 138) = 0.59, p = .738, \eta^2 = .025$), although somewhat larger exposure effects were observed over the right hemisphere. There was also no significant three-way interaction between hemisphere, site and exposure ($F(6, 138) = 0.96, p = .455, \eta^2 = .040$). Follow-up orthogonal contrasts showed that new-to-ERP IDs were less negative than both seen-in-sort-sIMG trials ($F(1, 23) = 13.29, p < .001, \eta^2 = .366$), and seen-in-sort-dIMG trials ($F(1, 23) = 18.78, p < .001, \eta^2 = .449$), and further that famous trials were more negative than both seen-in-sort-sIMG ($F(1, 23) = 7.77, p = .010, \eta^2 = .252$) and seen-in-sort-dIMG trials ($F(1, 23) = 9.84, p = .005, \eta^2 = .300$). There was no difference between seen-in-sort-sIMG and seen-in-sort-dIMG trials ($F(1, 23) = 0.82, p = .375, \eta^2 = .035$)¹. These main findings are shown in Figure 2.

Discussion

The present experiment explores the influence of experiencing within-person variability from ambient images during incidental face learning, using behavioural and ERP

¹ Please note that a corresponding ANOVA, in which two participants with error rates of more than 2 *SD* above the mean in the sorting task were excluded, yielded highly similar results. A significant main effect of exposure ($F(1, 21) = 14.51, p < .001, \eta^2 = .409$) was related to more negative amplitudes for seen-in-sort-sIMG, seen-in-sort-dIMG, and famous relative to new-to-ERP IDs (all $F(1, 21) > 13.26$, all $p < .002$, all $\eta^2 > .387$). Famous trials were more negative than both seen-in-sort-sIMG and seen-in-sort-dIMG trials (both $F(1, 21) > 6.24$, both $p < .021$, both $\eta^2 = .229$), and there was no difference between seen-in-sort-sIMG and seen-in-sort-dIMG trials ($F(1, 21) = 0.98, p = .332, \eta^2 = .045$).

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measures of familiarity. Whereas no familiarity effects were detected in the N170, we found that faces learnt through experience with natural within-person variability showed enhanced negativity, relative to novel faces, in the late N250 time range (280 – 400 ms), which is similar to previous results from explicit face learning experiments (Kaufmann et al., 2009; Schulz et al., 2012, Tanaka et al., 2006; Pierce et al., 2011). Of particular importance, N250 to same-exemplar and different-exemplar conditions were indistinguishable. We therefore conclude that an image-independent, or stable, representation was established during the sorting task, presumably as a result of exposure to natural variability of the newly learnt facial identities. Our ERP results are consistent with behavioural measures of familiarity (simultaneous matching task; Clutterbuck & Johnston, 2002; 2005), confirming earlier findings that experience of natural variability enables the formation of stable face representations. The present results are the first to demonstrate a corresponding effect in the N250, which has been previously linked to face learning, but has not been examined in a study that directly compared repeated and novel images of newly learnt faces. However, late N250 for newly learnt faces was less negative than N250 for famous faces, and larger negativity for famous but not newly learnt faces was also observed in the earlier N250 time window (180 – 280 ms). This suggests that the representations acquired during sorting were somewhat weaker and needed more time to be accessed compared to those for highly overlearned faces.

It is becoming increasingly clear that within-person variability should be considered, rather than controlled, when exploring face identification and face learning (Burton, 2013; Jenkins & Burton, 2011). By incorporating this natural variability into face learning procedures, we have recently found that experience of natural variability might in fact be necessary in order to form stable representations, as has been suggested by Bruce (1994). This requirement appears to arise because individuals have *idiosyncratic* variability, i.e. the

ways in which faces vary are different between identities (Burton, Kramer, Ritchie & Jenkins, 2016). Using the same behavioural matching task, but different target identities, we again found that simply experiencing natural variability between instances of the same person is sufficient to form representations that are sensitive to previously unseen images of that person (Andrews et al., 2015).

If such an incidental learning technique enables the formation of stable representations, one would expect that evidence of face representations would be evident from familiarity-sensitive ERPs. N250 has been shown to track the acquisition of new face representations formed from only one face image (e.g., Pierce et al., 2011; Tanaka et al., 2006, Wiese, Kaufmann, & Schweinberger, 2014) or from constrained variability (e.g., Kaufmann et al., 2009, Schulz et al., 2012). Importantly, however, no previous study examined effects of natural within-person variability on N250, which appears crucial for face learning (Bruce, 1994). We therefore substantially extend previous ERP findings to faces learnt from ambient images, with natural variability. Our finding of highly similar N250 amplitudes for same- and different-image conditions further shows that the resulting representations are identity- rather than image-specific. Moreover, we observed a later ERP face learning effect than previous studies (Kaufmann et al., 2009; Pierce et al., 2011; Schulz et al., 2012), suggesting that newly established stable representations derived from natural rather than restricted image variability are accessed at a somewhat later point in time.

Alternatively, the later effect could be driven by the implicit rather than explicit learning approach used in the present study – an idea that may be tested by subsequent research. At the same time, the finding of an earlier N250 effect for highly overlearned famous faces may suggest that access becomes more efficient with increasing experience with a particular facial identity.

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1 We argue that the increases in negativity would not occur for faces learnt from a
2 single image when tested with a different exemplar. There is strong evidence to suggest that
3 N250 is evident for faces learnt from one image when later tested with the same image
4 (Tanaka et al., 2006; Pierce et al., 2011), yet there is no evidence to suggest that seeing a
5 different image of a previously seen unfamiliar face results in greater N250 than faces that
6 have never been seen previously (Pfütze et al., 2002). In behaviour, learning faces from a
7 single instance does not result in good recognition of different instances of the face (Logie,
8 Baddely & Woodhead, 1987). Even learning faces from two different instances does not
9 reliably enable subsequent recognition when tested with a different image (Longmore et al.,
10 2008). These findings support our argument that experience of multiple images of the same
11 person is necessary in order to form stable face representations that are tolerant of natural
12 variability. It is therefore highly unlikely that greater N250 to new instances of faces seen in
13 the sorting task could result from single image learning, although this conclusion is not based
14 on empirical findings and therefore reflects an outstanding question for future research.

15 Our incidental learning procedure involves experiencing natural variability when all
16 images of that person are present simultaneously. This technique cannot fully account for
17 how faces are learnt naturalistically, as different instances can normally only be seen at the
18 same time if seen from photographs. Behavioural data in the present study also show some
19 evidence for identity learning even when different images of the respective person were not
20 seen at the same time; during the matching task, identities that were only seen during the ERP
21 task were recognized more accurately than completely novel identities. While naturally
22 varying instances of unfamiliar faces are often not identified as the same person (Jenkins et
23 al., 2011), the debilitating effects of variability can be overcome by providing the viewers
24 with the information that they should expect to see only two people. We suggest that
25 participants also expected this context during the ERP task for then novel faces; observers

1 had recently been informed that different face images were of only two different identities,
2 and during the ERP task saw two other identities who were already familiar. It is therefore
3 plausible that stable representations formed online for unfamiliar identities introduced during
4 the EEG part of the experiment. Overall, sequential presentation of faces with context
5 information maybe a promising new method for understanding how faces are learnt.

6 A notable finding from this experiment was the observation of graded familiarity,
7 both from ERPs and behaviourally. More specifically, late N250 for newly learnt faces was
8 more negative than for faces novel to the EEG part, but not as negative as for highly
9 overlearnt famous faces. Moreover, matching was best for faces learnt during the sorting task,
10 but was still better for identities introduced during the previous ERP part than for novel faces.
11 Under normal situations, it is likely that faces become increasingly familiar, as we have more
12 experience with them (Jenkins & Burton, 2011), and behavioural experiments on face
13 learning have begun to show such graded effects (Clutterbuck & Johnston, 2002; 2005). As
14 greater experience with faces necessarily means experience of more natural variability, it is
15 possible that graded effects of familiarity indicate a continued consolidation and refinement
16 of face representations. That is, with more instances comprising a representation, it becomes
17 less likely that non-identity specific information is erroneously encoded into any resulting
18 representation. We suggest that examining both behavioural and neural correlates of different
19 levels of familiarity might prove useful in developing a comprehensive understanding of face
20 processes underlying learning and identification.

21 In conclusion, the present study is the first to demonstrate a neural correlate of the
22 implicit formation of image-independent face representations, which were established using
23 an incidental learning technique with ambient images. Previous research has focussed on our
24 explicit *memory* for faces, and our ability to identify individual faces (Bonner et al., 2003;
25 Longmore et al., 2008; Reynolds & Pezdek, 1992). Here we addressed the question of how

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1 different instances of the same person are implicitly combined into a stable representation,
2 which may more closely resemble face learning in real life. We found an enhanced late N250
3 for implicitly learnt facial identities, reflecting access to new representations formed from
4 natural variability. We suggest that future research into face learning should consider how
5 between- *and* within-person variability contributes to the joint problem of telling faces apart,
6 while also telling faces together.

7
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1 2
3 1 Table 1. ANOVA results for ERP modulations at P1, N17 and P2
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Effect	Latency	<i>df</i>	<i>F</i>	<i>p</i>	ηp^2
P1	85-115				
Hemisphere		1, 23	1.77	.196	0.07
Exposure		3, 69	1.11	.351	0.05
Hemisphere x exposure		3, 69	2.42	.073	0.1
N170	130-160				
Hemisphere		1, 23	0.16	.693	0.01
Site		2,46	1.52	.229	0.06
Exposure		3, 69	1.01	.394	0.04
Hemisphere x site		2,46	1.29	.285	0.05
Hemisphere x exposure		3, 69	0.11	.954	0.01
Site x exposure		6, 138	1.94	.079	0.08
Hemisphere x site x exposure		6, 138	1.03	.409	0.04

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1 Table 2. ANOVA results for ERP modulations at Early and Late N250

Effect	Latency	<i>df</i>	<i>F</i>	<i>p</i>	ηp^2
Early N250 180-280					
Hemisphere		1, 23	32.60	< .001	0.59
Site		2,46	43.00	< .001	0.65
Exposure		3, 69	4.46	.006	0.16
<i>SIS-sIMG vs NTM</i>		1, 23	2.09	.162	0.08
<i>SIS_sIMG vs famous</i>		1, 23	5.13	.033	0.18
<i>SIS_dIMG vs NTM</i>		1, 23	3.09	.092	0.12
<i>SIS_dIMG vs famous</i>		1, 23	4.92	.037	0.18
<i>SIS_sIMG vs SIS_dIMG</i>		1, 23	0.03	.865	0.001
Hemisphere x site		2,46	6.77	.003	0.23
Hemisphere x exposure		3, 69	1.91	.135	0.08
Site x exposure		6, 138	1.12	.354	0.05
Hemisphere x site x exposure		6, 138	1.09	.373	0.05
Late N250 240-280					
Hemisphere		1, 23	35.67	< .001	0.61
Site		2,46	39.95	< .001	0.64
Exposure		3, 69	15.30	< .001	0.4
<i>SIS-sIMG vs NTM</i>		1, 23	13.29	.001	0.37
<i>SIS_dIMG vs famous</i>		1, 23	7.77	.010	0.25
<i>SIS_dIMG vs NTM</i>		1, 23	18.78	< .001	0.45
<i>SIS_dIMG vs famous</i>		1, 23	9.84	.005	0.3
<i>SIS_sIMG vs SIS_dIMG</i>		1, 23	0.82	.375	0.04
Hemisphere x site		2,46	2.66	.081	0.1
Hemisphere x exposure		3, 69	0.59	.624	0.03
Site x exposure		6, 138	0.76	.603	0.03
Hemisphere x site x exposure		6, 138	0.96	.455	0.04

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3 1 **Figure Captions**
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6 3 *Figure 1.* Examples of ambient face images from two identities.
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9 4
10 5 *Figure 2.* Early- and late-N250 ERP modulations across temporal and occipital-temporal sites
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12 6 for left and right hemispheres, showing mean amplitudes by exposure
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15 7 *Figure 3.* Scalp-topographical voltage maps (spherical spline interpolation, 110° equidistant
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17 8 projection) of the different waves between new-to-ERP and previously seen face identities.
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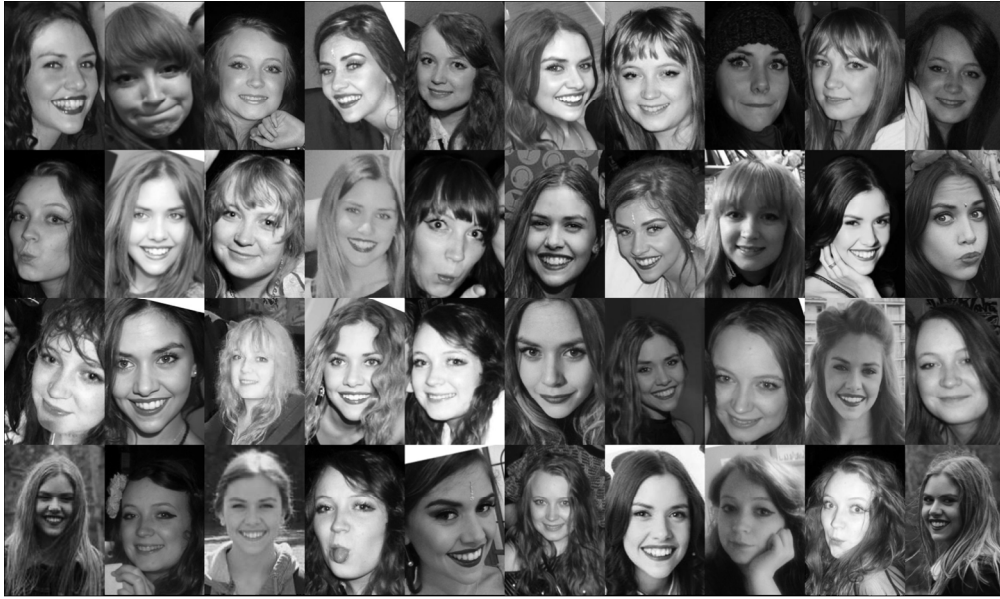


Figure 1

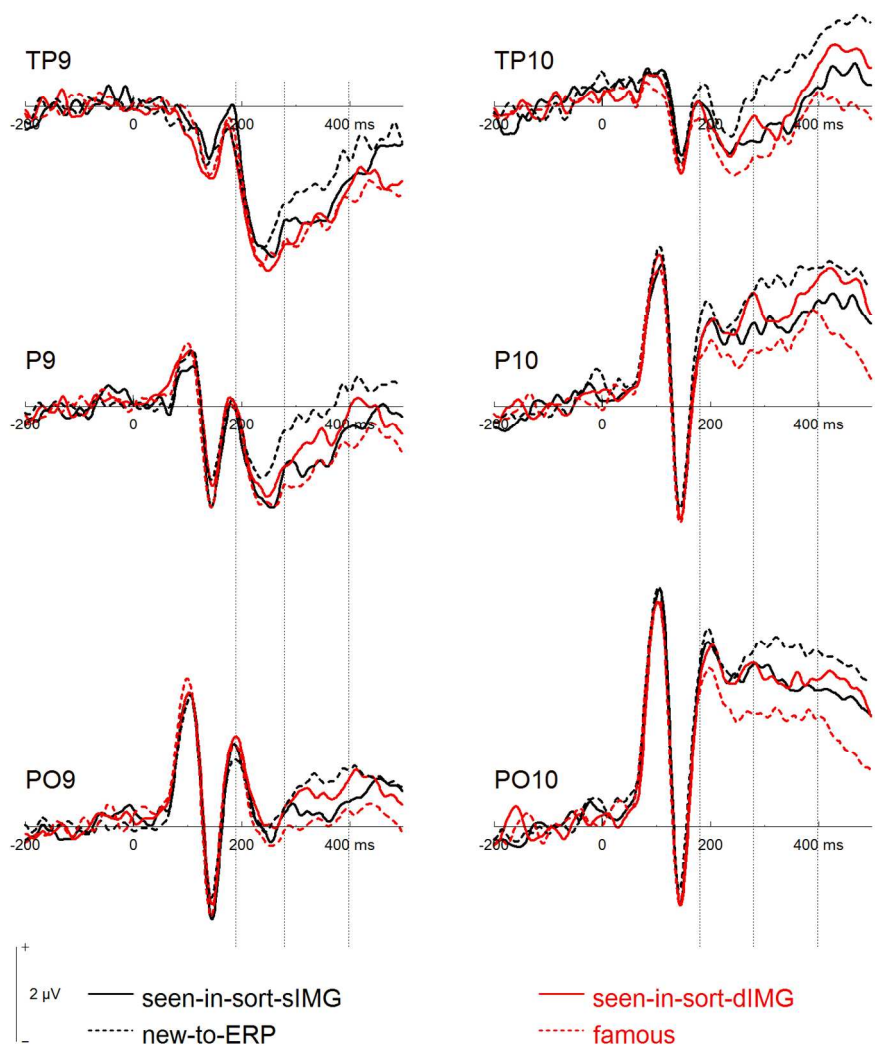


Figure 2

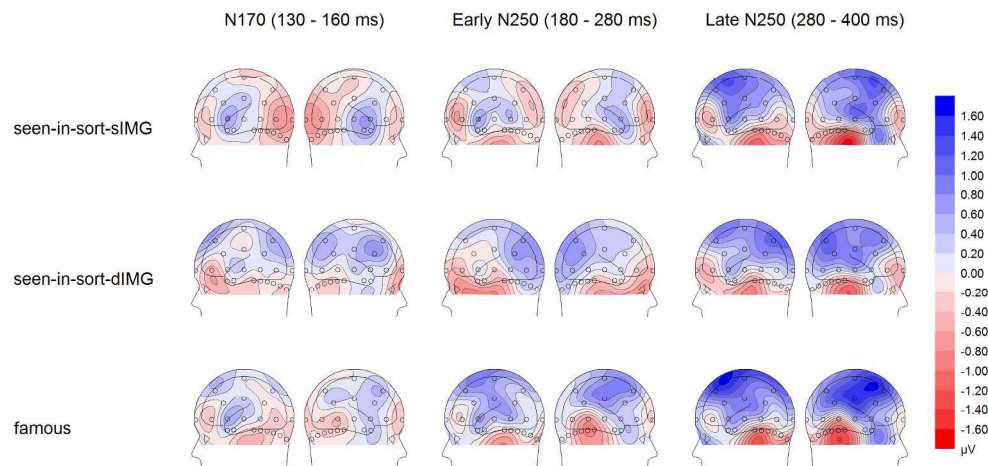


Figure 3
846x448mm (72 x 72 DPI)